FIELD TESTS OF THEORIES CONCERNING DISTRIBUTIONAL CONTROL[1]

THE conditions of animal distribution and the causes of these conditions are facts which concern intimately the problems of the persistence and of the evolution of species. The present writer believes that the field naturalist is in a position to contribute in large measure toward the solution of these problems, and it is the purpose of this paper to show how comparative studies in the distribution of species may throw light not only upon the nature of the environmental complex, but also on the relative importance of its various component factors.

Some simple facts of distribution which are of common observation, and which were early recorded by the systematic zoologist, are: (1) that each animal occupies a definite area, that is, has a habitat or range, which is distinctive enough to be included among the characters of the species and described along with its habits and the features of its bodily structure; (2) that some species (and even some of the higher systematic groups) range widely, and cover great extents of country, while others are extremely local or restricted in their distribution; and (3) that, notwithstanding considerable variation in this degree of distributional restriction, many species (or higher groups) are found nearly or entirely to coincide in range, so that sets of species, of varying ranks, may be recognized distributionally, as constituting realms, zones, faunas, subfaunas, associations, etc.

Perhaps the most prominent delimiting factor, and the one which has been emphasized through repetition in the early systematic writings, is the obvious one of physical barriers—represented by bodies of water in the case of the terrestrial species and by land in that of the aquatic. The majority of animals inhabiting islands and seas are specialized in such a manner as to be hemmed in by the limits of their respective habitats. Individuals overstepping the barrier in either case are subject to prompt destruction. This obvious type of distributional control has always been and will remain an important one for consideration; but with the acquisition of detailed knowledge regarding the distribution of animals on large continental areas, naturalists have been led to propose many other factors which

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have seemed to them to prevent the random and unrestricted spreading of animals over the surface of the land. The following is a list of the factors which various writers have nominated as affecting the distribution of the higher vertebrate animals. This list is complete only to the extent that my own examination of the literature is so. Many of the items have been found in dissertations upon bird migration, which is, of course, but one phase of the general subject of distribution.

Vegetation.
Food supply, kind and quantity.
Rainfall.
Humidity of the air (relative or absolute).
Wetness or dryness of the soil.
Barometric pressure, or altitude.
Atmospheric density.
Safety of breeding places.
Availability of temporary refuges.
Water (to land species).
Land (to aquatic species).
Nature and availability of cover, or shelter from enemies.
Nature of the ground (coarse or fine soil, or rock).
Insolation, or light intensity.
Cloudiness.
Temperature: in general; mean annual; of winter; of period of reproduction; of hottest part of year.
Interspecific pressure, or competition, or race antagonism.
Parasitism.
Individual, or racial, preferences.

It is at once plain that some of the items enumerated are extremely complex, and that the most superficial analysis will show some duplication among them. For example, the factor of vegetation as influencing the distribution of different mammals resolves itself principally into the elements of food-supply and shelter, and, subordinately in most cases, into those of temperature, humidity, and nature of the soil. As some of the suggested factors may really never function in any vital degree as supposed, the total number of really critical factors is probably smaller than the total of the items just listed. Time could not here be taken to discuss the intrinsic nature of each elemental factor, even if the writer were equipped to handle such a variety

of subjects; for such a discussion would in most instances lead directly into physics and chemistry, and into a study of the physiological processes of the animals affected by each of these factors. I should, however, like to dispose at once of one of the "factors" listed, and which I hear and see repeatedly cited as a cause of restriction in distribution—particularly in that of birds.

Many people claim to see in the facts of distribution only the operation of a *preference* on the part of each animal—by virtue of which, if a heterogeneous lot of animals were introduced into an area presenting diverse conditions, each species would *choose* its "natural" surroundings and rapidly allocate itself in a normal way. I grant that such a choice would almost certainly be made. In fact the hypothesis is being proved continually all over the country in connection with the migration of birds. Scores of species travel north in the spring to countries for a preceding interval unoccupied; and while, roughly speaking, they travel together, and arrive together, they segregate themselves, immediately on their arrival, and repair to separate sorts of ground, each species by itself: the pipits to the prairie, the water-thrushes to the streamside thicket, the black-poll warblers to the spruce forest, and so on. We have here an obvious choice exercised in the selection of habitats. But does this segregation of species by exercise of "individual preference" in a uniform direction change the nature of the problem in any fundamental way? Should we not here recognize merely a character in the cerebral equipment of each race, which, like every external peculiarity in its structure, is in considerable measure the result of protracted impress upon the organism from the environmental complex of factors to which the race has been subject through past time? There is no other additional factor than those environmental ones (plus the intrinsic fixedness of the species, within certain limits of plasticity, and the "evolutionary momentum") to be called into account.

As to the mechanism of geographic limitation, the adjustments to the various critical factors are inevitably forever in process, though reduced to a minimum at times of slow environmental change. The refined method of individual "preference" or "choice" is superior to the wasteful process of wholesale destruction which would be experienced by individuals finding themselves out of place as the result of a haphazard selection of

locality. The frontier individuals, those on the margin of the habitat of the species, may not prosper as greatly, or reproduce as prolifically, as those in the metropolis of their species; but they certainly do not, as a rule, beat themselves to death individually against their limiting barrier, of whatever nature it may be.

To resume the main topic of this discussion, I shall attempt to show that it is possible from field observation to indicate in the case of certain species, some, at least, of the factors which control their distribution; and further that we who live in California have splendid opportunities to gather and examine data by means of which the general laws of animal distribution can be determined. An area within comparatively easy reach presents a wide diversity in topographic and climatic features. Occupying this area is an abundant complement of the higher vertebrate classes. Within the political limits of the state, systematists now recognize the presence of 388 species of mammals, 543 of birds, 79 of reptiles and 37 of amphibians. We have plenty of material to work with. I shall proceed to discuss a few selected species about which we seem to have knowledge enough to warrant provisional inferences.

THE CASE OF THE OREGON JAY

The Oregon jay (*Perisoreus obscurus*), a close relative of the Canada jay, or whisky-jack, occurs in California only in the northern third of the state. Even there it is very local in its occurrence and absolutely non-migratory. On the Warner Mountains, Modoc County, it ranges from the highest parts down to 7,000 feet altitude. On Mount Shasta it ranges from near timberline down to about 6,000 feet altitude. It is absent for a long distance to the west, through the Trinity mountain mass, but it recurs along the seacoast of Humboldt County, within fifteen miles of the ocean. And here is the curious point: along this coast strip it does not range higher than 300 or 400 feet above sea level, although there are mountains not far inland which rise to an altitude of several thousand feet. Let us look into this case for the purpose of determining the factors responsible for this interrupted range.

The Oregon jay, like most members of the crow family, is not restricted in diet. It eats a great variety of both vegetable and animal substances; its food varies in character according to season and local conditions. The supply of any particular kind

of food is not likely, therefore, to be a controlling factor in its distribution.

The bird is a forest dweller. Its equipment as regards manner of flight and course to take in case of attack by enemies is adjusted to a forest habitat, and nowhere within the writer's knowledge does this jay extend its range beyond the limits of woods of some sort. Although somewhat predaceous itself, it has regular enemies among hawks and owls, for protection from which it makes use of forest vegetation. This factor of forest cover, then, must be counted as essential. But the range of the bird is not continuous wherever forests extend.

In the interior of California it does not descend below a certain altitude. Now three other factors in its distribution are quite obviously connected with that of altitude, namely, barometric pressure, atmospheric density, and temperature. But when we take into account the fact that the Oregon jay exists at or close to sea level around Humboldt Bay, the first two factors, those of pressure, and air density, are instantly eliminated, because of the obvious fact that the bird successfully maintains itself in localities of widely differing altitude where these factors are thus extremely diverse.

With reference to temperature, we know without recourse to instrumentation that there is a decrease upwards at an average rate of 3 to 4 degrees F. per thousand feet. If, then, the bird is limited downwards at a critical point, the inference apparently follows that temperature is the determining factor, and this conclusion is inevitable if we consider only Mount Shasta and the Warner Mountains. But the bird's occurrence at Humboldt Bay complicates the problem. In order to reconcile these facts of distribution we must look into the situation with reference to season. On doing so we discover that the home of the Shasta and Warner jays is subject to severe winters with heavy snow, very much colder than the winters at Humboldt Bay, where the climate is equable and snow rarely falls. But the summer temperature at Humboldt Bay is well known to be much cooler than that of even somewhat higher regions in the interior, up to an altitude of at least 4,000 or 5,000 feet, because of the eastward moving air-currents, which are coolest where they first leave the sea surface and warm up as they pass farther and farther inland. We are therefore led directly to the final inference that the summer temperature at sea level about Humboldt Bay

closely approximates the summer temperature at from 6,000 to 9,000 feet on Mount Shasta and above 7,000 feet on the Warner Mountains. In these three areas, the air is cooler in summer than in the interlying areas and thus better adapted to the finely adjusted requirements of the Oregon jay. *Summer* temperature, between certain degrees, is one critical factor.

Three more factors present themselves for consideration in connection with the Oregon jay, those of humidity, rainfall and cloudiness. Humboldt Bay lies in the most humid and continuously rainy section of California. Mount Shasta and the Warner Mountains are relatively arid, the latter most notably so. It would appear, therefore, that humidity, rainfall and cloudiness had little or nothing to do with cutting off the range of this bird, though one or other of these factors may have been responsible for the very slightly darker tone of color which distinguishes the coast jays (subspecies *Perisoreus obscurus obscurus*) from those in the interior (*P. o. griseus*). But, however this may be, it is clear that temperature must dominate greatly over the three factors named in checking dissemination.

In summary, we may therefore dispose of the following factors as having little or no effect on the distribution of the Oregon jay as a species: the nature or quantity of its food supply, atmospheric density and pressure, cloudiness, rainfall, humidity of the air or soil, and winter temperature. This eliminates all but the two factors: shelter of a sort provided by the forest habitat, and temperature of the summer season.

THE CASE OF THE CONY

The cony or pika is a mammal represented in California by four quite similar races (*Ochotona taylori, O. schisticeps schisticeps, O. s. muiri,* and *O. s. albatus*), which agree distributionally in occupying a very restricted habitat along high mountain crests. I know of no place in central California where conies range below an altitude of about 8,000 feet, and they range upwards to fully 12,000 feet in the vicinity of Mount Lyell. They thus occupy an altitudinal belt between extremes 4,000 feet apart. With regard to zones of vegetation conies live from considerably below timberline to considerably above timberline. Extended observation shows that their existence is in no way correlated with that of trees or shrubs of any sort. Like their relatives, the rabbits, they feed entirely on low vegetation, biennials mostly;

but unlike most kinds of rabbits they are strictly dependent for safety from enemies upon rocks, especially where these are loosely piled as in talus slopes and so afford deep retreats within their interstices. The whole equipment of a rabbit is clearly adapted to foraging in the open, its keen hearing and eyesight quickly warning it of the approach of enemies, and giving it time to escape by means of its unusual running powers. But the cony is equipped in a very different way, as it has relatively small ears and eyes, and small hind legs. It is compelled to forage close to or beneath cover. In fact in field observations it is rarely seen on the move except momentarily, and then only between or beneath angular granite blocks, where it grazes on such little patches of vegetation as are within immediate reach.

It is clear from numerous observations that the cony is sharply restricted in a large part of its range by the rock-pile habitat. Even at favorable altitudes it is not found away from this refuge. There are obviously, however, one or more additional factors in its distribution. In many parts of the Sierras, talus slopes occur from near the highest summits down to the foothills. As examples of these, one may cite the vast earthquake taluses of the Yosemite Valley proper, which occur almost continuously down to and below the 4,000-foot contour. These taluses have been searched diligently both by trapping and hunting, without our naturalists finding a trace of conies below 8,000 feet. The animals are easy to detect, by reason of their characteristic cry, uttered at any time during the day, though more particularly in the morning and the evening, and by the accumulations of their feces, the pellets constituting which are, in size, shape and texture, unlike those of any other mammal. What is it, then, that limits the conies downward on the western flank of the Sierras, where their necessary rock habitat is continuous, and where food of the right sort is also continuous? Let us try barometric pressure, and atmospheric density, which may properly be considered together. These conditions change sensibly with altitude and, if we take into account California alone, the facts would seem to entitle them to serious consideration as active delimitors of the conies downward. But as we trace the range of the conies far to the northward we are led to a different conclusion. The altitudinal limits of their range is found to descend quite regularly towards the north, until, in the case of one race, even sea level is reached, at Bering Sea. Clearly, conies, generically, are

thus proven not to be affected by atmospheric pressure, or by atmospheric density, at least in as far as it is modified by altitudes up to 12,000 feet. The same fact—depression of range towards the north—discloses a third concomitant of altitude, which is also a concomitant of latitude, namely, temperature, and this is beyond doubt the determining factor. As the isotherms dip toward sea level to the northward so does the range of the genus *Ochotona*. We have, therefore, by study of geographical distribution in this case established two important controlling factors, namely (1) safety refuges of a sort provided by talus slopes and glacial moraines; (2) temperature, at least downward below the degree, correlated in the mountains of California by a mean annual or summer computation or for a briefer period at the time of reproduction, with an altitude of eight to twelve thousand feet, according to latitude, slope exposure and air currents.

It is not possible for one to say from the data in hand what the direct controlling factors of the upward limits of the cony's range may be. Taluses extend up to the highest peaks, but there is no growth of grass above about the 12,000-foot contour even on the most favorable slopes. As the disappearance of the cony in the higher altitudes is coincident with the disappearance of its food, it appears as if failure of food alone were the delimitor here; but we have no way of showing that even if food did continue the cony would be restricted upward, as it certainly is downward, by a change in temperature beyond some critical point. The cause of its delimitation downward, however, remains clear.

THE CASE OF THE ROSY FINCH

In the case of the bird called generically *Leucosticte,* or rosy finch, we find a condition astonishingly similar to that of the cony. In fact almost the entire preceding account could be made relevant here, by merely substituting the term rosy finch for cony. The ranges, altitudinal and geographical, of the two animals are almost identical. The only obvious differences appear in their ecologic relations, and consist in the lesser dependence of the bird upon shelter and in the dissimilar nature of its food. The rosy finch forages gregariously on the open slopes, near timberline and above, though its nest is hidden away in the clefts of rock ledges and taluses. It shuns the trees

and bushes even where it ranges well below timberline. It feeds winter and summer upon seeds of dwarfed vegetation, including those of grass and herbs of various sorts. As far as I can see, its food and feeding habits are identical with those of such other fringillids as goldfinches and siskins. Yet the leucosticte, by the same tests as were used with the cony, is beyond any contention limited downward by an increase of temperature. We find the bird to possess various adaptive features in common with certain arctic finches, such as tufts of bristle-like feathers over the nostrils to prevent fine snow from entering. These enable the bird to spend the long winter on the cold wind-swept ridges, but at the same time would hardly prevent the bird's dropping to warmer climes if the heat were not a strongly deterrent factor.

Cases of coincidence, as instanced by that of the cony and leucosticte, among animals of widely different powers of locomotion and ecologic position, are the rule, not the exception, and impel the observer to belief in the efficacy of the controlling factor above mentioned.

The Case of the Redwood Chipmunk

The redwood chipmunk (*Eutamias townsendi ochrogenys*) is an animal confined to a very narrow but exceedingly long distributional area extending south from the Oregon line as far as Freestone, Sonoma County. Throughout this belt it is conspicuously numerous, and is usually the only species of chipmunk present, so that the limits of its range have been easy to mark definitely along the several lines explored. This rodent, by various geographic tests similar to those I have recounted for other birds and mammals, is clearly delimited away from the coast at the bounds of the well-known fog-belt to which the redwood tree and numerous other plants as well as animals belong. The chipmunk, however, depends in no way upon the redwood or any other one plant species as far as I can see, but feeds upon a great variety of seeds and fruits, like many of its congeners elsewhere.

That temperature is also a delimiting factor is shown in parts of the range of the redwood chipmunk. But atmospheric humidity or cloudiness or rainfall, factors which I have in this case failed to dissociate, together constitute or include the chief controls.

THE CASE OF THE BELTED KINGFISHER

It is to be observed that specialization for getting a particular kind of food invariably brings with it restriction of range to the territory providing that kind of food. The northwestern belted kingfisher (*Ceryle alcyon caurina*) is a good example of this. In California we find this bird present at various times of the year both along the seacoast and along various fish-supporting streams, from the Colorado River to the Klamath River and up the mountain streams to at least as high an altitude as Yosemite Valley. The kingfisher is seen during migration in many places away from streams, but it tarries at such times only where its natural diet can be procured, as, on occasion, at fish ponds in city parks. There is a unique instance of a kingfisher observed on the desert catching lizards, but exceptional occurrences of this kind are of course not to be given consideration in making generalizations.

It is observable further in regard to this species of kingfisher, that it must have earth banks in which to excavate its breeding tunnels. Lack of these along any stream, otherwise favorable, prevents the bird from staying there through the season of reproduction. Furthermore, there is also obvious temperature restriction; for, given a fish-producing stream, with banks apparently well suited for excavation of nesting places, such as is the Colorado River and its distributaries, and the summer temperature must be at least below that of southern California south of the 35th parallel. That all such streams are well supplied with kingfishers in winter, and are forsaken only during the hot summer, seems to show that a relatively cool temperature is for them in some way or another essential to successful reproduction.

We find, then, in the case of the belted kingfisher, that the factors of a requisite kind of food, and a requisite kind of nesting place, both having to do with the structural powers and limitations of the bird, together with the factor of the temperature of the summer season, are those that account for the distribution of the species within the state of California, as we find it.

THE CASE OF THE MEADOWLARK

The western meadowlark (*Sturnella neglecta*) is a bird of relatively omnivorous diet. Note that I say relatively, for the word omnivorous unmodified would apply only to such an ani-

mal as would eat the sort of food that any animal eats, and this is an obvious impossibility for the meadowlark when we consider such uncommon articles of diet as wood and petroleum. Compared with many other birds, the meadowlark does use as food a very wide range of plant and animal objects. This food, however, is restricted to a particular habitat source, namely to the meadow. The bird's entire equipment specializes it for successful food-getting and for escape from enemies upon a grassy plain or meadow. And it is a matter of common observation that its range is sharply delimited in most directions at the margin of the meadow habitat, as where this is interrupted by forest, brushland, marsh, rock surface or sand flat. This is a conspicuous example of what we may call associational restriction. But it is not the only way in which the meadowlark is hemmed in. In this connection California again provides critical distributional evidence.

We find meadowlarks occupying practically every appropriate meadow, large and small, from the Mexican line to the Oregon line and from the shores of the Pacific to the Nevada line, *except* above a certain level on the higher mountains. In traveling up the west flank of the Sierras, and this I have now verified along three sections, meadowlarks cease to be observed at approximately the 4,500-foot level, and this in spite of the fact that above that altitude meadows are found which are to all appearances ideal for meadowlark requirements. I need only refer to such seemingly perfect summer habitats as Monache Meadows and Tuolumne Meadows. And though, in the winter these would be uninhabitable, so are other meadows (as those in the Modoc region, for instance), which are in summer warm and at that season abundantly inhabited by meadowlarks. By the elimination then upon proper grounds of various factors from the list, we have left only three possible factors in this upward delimitation, namely, decreased atmospheric pressure, decreased air density and decreased temperature of the summer season. Since meadowlarks exist at corresponding altitudes in the warmer though elevated Great Basin region, and since it has been possible to eliminate positively and in a similar way the first two factors in the cases of many other birds and mammals, these factors are presumably without influence on the meadowlark; and there is left but one—temperature.

Within the state of California, meadowlarks, without the

slightest detectable subspecific modification, thrive under both the cloudy, humid conditions of the northwest coast belt and under the relatively cloudless, arid conditions of Owens Valley. Factors of humidity, of air and soil, cloudiness, and light intensity, seem to avail nothing in checking their spread. With such a degree of associational specialization as is exhibited by these birds there is little chance of a serious competitive struggle with other vertebrates, and no evidence of such has been observed. As far as California is concerned, the meadowlark's range is thus only limited associationally and zonally, that is by the extent of its particular meadow habitat and by diminished summer temperature below some critical point.

The meadowlark well illustrates some further facts with regard to distribution. In California it is unquestionably on the increase as regards total population. This is due chiefly to the great extension of habitable territory resulting from man's occupancy and cultivation of the land, bare plains, brushlands and even woods being replaced by irrigated alfalfa and grain fields. These the meadowlarks find suitable and invade because of their expansive reproductivity, and soon populate to the fullest extent permitted by the minimum annual food supply. In other words, associational barriers have moved, to the advantage of this particular bird, though at the same time to the disadvantage of endemic species of different predilections. I should estimate that the total meadowlark population in the San Joaquin-Sacramento basin is now fully three times what it was thirty years ago.

Animal distribution is not fixed. It changes with the shifting of the various sorts of barriers, and doubtless also as a result of a gradual acquisition by the animals themselves of the power to overstep barriers, as by becoming inured to greater or lesser degree of temperature. The power of such accommodation, or inherent plasticity, evidently varies greatly among different animals; and at best its operation is very slow. Many species have proved stubborn and have been exterminated, as the factor-lines, or barriers, shifted. By the shifting of, say, two critical factor-lines towards one another, the existence of a species may have been cut off as by a pair of shears.

SUMMARY

In this paper I have enumerated various factors thought to be concerned with the control of the distribution of vertebrate animals. A number of birds and mammals have been cited to show how we may use our more or less detailed knowledge of their ranges so as to demonstrate the operation of one or several out of the many possible factors as limiters to distribution. The method employed is one of examination, comparison and elimination, applied to all parts of the margin of animals' ranges. The range of any one animal must be examined at all points of its periphery in order that all of the factors concerned may be detected. One factor may constitute the barrier in one section of the periphery of the range of a species, a totally different factor in another section.

The results of the geometric ratio of reproduction would bring about areas of occupancy in the shape of perfect circles. But we never find such symmetrical ranges. The very fact that the outlines of the ranges of animals are extremely irregular is significant of the critical nature or inexorableness of the factors which delimit them. These factors have to do with the evolution, persistence and extermination of species.

Note that we always have to take into account, in attempting to discern factors of limitation, the animal's own inherent structural equipment. This prescribes restriction at once in certain regards. Referring again to our list of suggested factors, we find the long-emphasized ones of land to aquatic species and bodies of water to terrestrial species really presenting an extreme manifestation of associational restriction. Food source, methods of food-getting and safety refuges are involved.

It is to be noted further that the factors are various and that the most important factor for one species may prove of little effect with another species. Species do not react uniformly to the same environment. It is undoubtedly always a combination of factors which accounts for an animal's geographic range in all parts of the periphery of that range. It is most certainly never one factor alone. No one will claim that temperature is the *only* delimiting agent in controlling vertebrate distribution; nor could this claim be made for humidity alone, or for food supply alone, or for safety of breeding-places alone.

Given a large continuous area, however, as upon the North

American continent, one single factor does happen to loom up as being the most frequent delimiter of distribution, or even the ultimately effective one, in greater or less degree, even though other factors be effective also. This factor is temperature. The cases cited illustrate the tenet that in some direction or another, temperature beyond certain limits, up or down, cuts off further dissemination. This is part of the basis of the life-zone idea. But, as I have tried to bring out above, this fact is in no way antagonistic to the claim that other factors, as of humidity, food supply, and shelter, also figure critically, giving a basis for recognizing faunal areas and associations. Finally, if our discussion of the subject has been sound, it is evident that data secured through field observation can be so employed as to bring results essentially similar to, and as conclusive as, those secured through laboratory experimentation.

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